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SOCIAL LIFE AMONG THE NSECTS[1]

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LECTURE I

GENERAL REMARKS ON INSECT SOCIETIES. THE SOCIAL BEETLES

DURING the past fifty years, the science of living organisms has itself, like a living organism, developed so rapidly that it has more than once changed its aspect and induced its votaries to change their points of view. The future historian of the science will probably emphasize the difference of attitude towards the living world exhibited by Darwin and his contemporaries and that of the present generation of twentieth century biologists. He will notice that the works of the Victorians abound in such phrases as the " struggle for existence," "survival of the fittest," "Nature, red in tooth and claw," and disquisitions on the unrelenting competition in the development, growth and behavior of all animals and plants. This struggle, as you know, was supposed to constitute the very basis for the survival of favored forms through natural selection. There can be no doubt that even to-day we must admit that there is much truth in all this writing, but we would insist that it depicts not more than half of the whole truth. To us it is clear that an equally pervasive and fundamental innate peculiarity of organisms is their tendency to cooperation, or "mutual aid," as it was called by Prince Kropotkin. Even to the great Victorian naturalists the fact was familiar—though they failed to dwell on its great social significance—that all living things are genetically related as members of one great family, one vast, living symplasm, which, though fragmented into individuals in space, is nevertheless absolutely continuous in time, that in the great majority of organic forms each generation arises from the cooperation of two individuals, that most animals and plants live in associations, herds, col-

[1] Lowell Lectures.

onies or societies of the same species and that even the so-called "solitary" species are obligatory, more or less cooperative members of groups or associations of individuals of different species, the biocœnoses. Living beings not only struggle and compete with one another for food, mates and safety, but they also work together to insure to one another these same indispensable conditions for development and survival. The phenomena of mutualism and cooperation are, indeed, so prevalent among plants and animals and affect their structure and behavior so profoundly that there has arisen within very recent years a new school of biologists, who might be called "symbiotists," because they devote themselves to the investigation of a whole world of microorganisms which live in the most intimate symbiosis within the very cells of many if not most of the higher animals and plants.

If asked why it seems advisable to devote six lectures to social life among the insects, I might say that these creatures exhibit many of the most extraordinary manifestations of that general organic cooperativeness which I have just mentioned, and that these manifestations have not only an academic but also a practical interest at the present time. For if there is a world-wide impulse that more than any other is animating and shaping all our individual lives since the world war, it is that towards ever greater solidarity, of general disarmament, of a drawing together not only of men to men but of nations to nations throughout the world, of a recasting and refinement of all our economic, political, social, educational and religious activities for the purposes of greater mutual helpfulness. As Edward Carpenter says:

> The sense of organic unity, of the common welfare, the instinct of Humanity, or of general helpfulness, are things which run in all directions through the very fibre of our individual and social life—just as they do through that of gregarious animals. In a thousand ways: through heredity and the fact that common ancestral blood flows in our veins—though we be only strangers that pass in the street; through psychology, and the similarity of structure and concatenation in our minds; through social linkage, and the necessity of each and all to the other's economic welfare; through personal affection and the ties of the heart; and through the mystic and religious sense which, diving deep below personalities, perceives the vast flood of universal being—in these and many other ways does this Common Life compel us to recognize itself as a fact—perhaps the most fundamental fact of existence.

The social insects may also be singled out for special treatment for the following more particular reasons: first, because they represent Nature's most startling efforts in communal organization and have therefore been held up to us since the days of Solomon as eminently worth imitating, or to be avoided as an "abschreckendes Beispiel"; second, because these organizations are simpler and more perspicuous than our own and we can study their origin,

development and decay and subject them to experimentation; third, because many of them represent clean-cut products of comparatively simple evolutionary tendencies and hence final and relatively stable accomplishments; fourth, because they show us the extent to which social organization can be developed and integrated on a purely physiological and instinctive basis, and by contrast therefore throw into sharper relief some of the defects and virtues of our own more intellectual type of society; and fifth, because they are so remote from us that we should be able to study them in an unbiased and truly scientific spirit.

I wish to dwell somewhat on the third of these reasons for the purpose of placing in clearer perspective the great antiquity and completeness of the social organization of insects. Some years ago the museums of Königsberg and Berlin sent me for study an extraordinary collection of ants in lumps of Baltic amber. There were 9,560 specimens, representing 92 species and 43 genera. As you know, the Baltic amber is merely the fossil resin of pines which flourished during Lower Oligocene Tertiary times in the region which is now Sweden. The liquid resin exuded from the tree- trunks precisely as it does to-day, and great numbers of small insects, especially ants, were trapped in the transparent, viscid masses which hardened, fell from the trees or remained after the rotting of the wood and were carried down by the streams and embedded in what is to-day the floor of the Baltic Sea and the soil of Eastern Prussia. The lumps are now brought to the surface either by mining or by the action of the waves which cast them up on the beaches. So beautiful and lifelike are the insects preserved in the amber that by comparison all other fossils have a singularly dull and inert appearance. Many of the specimens which I was able to examine were as exquisitely preserved as living ants embedded in Canada balsam by some expert microscopist. My study showed conclusively that the ants have undergone no important structural modifications since the Lower Oligocene, that they had at that time developed all their various castes just as we see them to-day, that their larvæ and pupæ were the same, that they attended plant-lice, kept guest-beetles in their nests and had parasitic mites attached to their legs in the very same peculiar positions as in our living species, and that at least six of the seven existing subfamilies and many of the existing genera were fully established. Some of the species in the amber were even found to be practically indistinguishable from those now living in Northern Europe and North America. The Baltic amber also contains social bees, wasps and termites, and though these are not so well known, what I have said of the ants will also *mutatis mutandis* prove to be true of them. Since my work was published Cockerell and

Donisthorpe have described a number of ants from the Bagshot Beds of the Isle of Wight, also of Oligocene age, and very recently Cockerell has described a typical ant, *Eoformica eocenica,* from even earlier strata, the Green River Eocene of Wyoming. We must conclude, therefore, that these insects—and the same is very probably true also of the wasps, bees and termites—had their origin in the Cretaceous, if not earlier. What I wish to emphasize is the fact that all the main structural and social peculiarities of these insects were completed by the beginning of the Tertiary and that they have since been merely marking time or developing only the slight modifications which serve to distinguish genera, species, subspecies and varieties.

Now how many years have elapsed since the beginning of the Tertiary? Geologists have, of course, made many and diverse estimates. I shall take the most recent, which are much in excess of earlier computations. Barrell gives the time since the beginning of the Tertiary as 55 to 65 million years. But the social insects are the most recent—the mere newly rich, so to speak—in the great class Insecta, which has a fossil record extending back to the Upper Carboniferous. And as our earliest known fossils are perfectly typical insects, it is probable that the earliest Hexapods made their appearance in the Silurian, if not earlier. This would make the period during which these wonderful creatures have been living and multiplying on our planet about 300 million years!

In order that we and the impatient reformers in our midst may experience the proper feeling of humility let us now compare the age of man and his society with that of the ants. During the Oligocene and early Miocene, while these insects, together with the uncouth primitive mammals, represented the dominant animal life of the plains and forests of the globe, the early Primates were just splitting into two tribes, one of which was destined to produce the modern apes, the other the Hominidæ, or humans. Our ancestors were probably just forsaking that life among the tree-tops which, as Woods Jones has shown, has left its ineffaceable impress on all the details of our anatomy. A large part of the diet of these early Hominids and their immediate ancestors probably consisted of those same ants which had already developed a cooperative communism so complete that in comparison the most radical of our bolsheviks are ultra-conservative capitalists. By a hundred thousand years ago our ancestors had reached the stage of the Neanderthal man, whose society was probably somewhat more primitive than that of the Australian savage of to-day. And so far as the actual, fundamental, biological structure of our society is concerned and notwithstanding its stupendous growth in size and all the tinkering to which it has been subjected, we are still in much

the same infantile stage. But if the ants are not despondent because they have failed to produce a new social invention or convention in 65 million years, why should we be discouraged because some of our institutions and castes have not been able to evolve a new idea in the past fifty centuries?

I find that social habits have arisen no less than 24 different times in as many different groups of solitary insects. Careful investigation of the life-histories of tropical species will probably increase this number. These 24 societies, which I propose to consider in more or less detail in this and the following lectures, represent very different stages in the evolution of the social habit. Some of them are small and depauperate, mere rudiments of societies, some are extremely populous and present great differentiation and specialization of their members, whereas others show intermediate conditions. And while each of the 24 different societies has its own peculiar features, we nevertheless observe that all of them have arisen in the same manner and have the same fundamental structure. Each is a family consisting of two parent insects and their offspring or at least of the fecundated mother and her offspring, and the members of the two generations live together in more or less intimate, cooperative affiliation. During the long history of the Insecta this situation has developed time and time again and quite naturally out of the very general propensity of female insects to lay their eggs on food suitable to the hatching larvæ or to make protective structures or burrows, to store them with food and to oviposit on it. As a rule, the mother insect then dies and never sees her offspring, but all such parental care, which is also very prevalent among many other animals and even among plants, is nevertheless a potential or implicit nursing or fostering, which readily become actual or explicit in such species as manage to survive the hatching of their young and can therefore continue to feed and protect them. It is difficult, nevertheless, to draw a hard and fast line between certain solitary forms and some of the societies or families I have selected, for there is a finely graded series of cases of parental care between complete indifference to the offspring and the families of what may be called the incipiently social or subsocial forms. As the societies grow in size and complexity they naturally change from associations in which the progeny depend on their parents to associations in which the parents come to depend on their progeny.

John Fiske and others have claimed that human society has been rendered possible by a lengthening of infancy and childhood, since this obviously involves more elaborate care of the young by the parents and a greatly increased opportunity of learning on the part of the child. This is true, but it is equally true that the adult

life of the parents must also be prolonged to cover the retarded juvenile development, and the insects show us that the lengthening of the adult stage comes first and makes social life possible. In solitary insects, of course, it is just the brevity of adult life that prevents the development of the social habit, no matter how long the larval period may be. This period may, in fact, extend over months or even years in certain insects which have an adult stage of only a few days or hours.

Momentous consequences necessarily follow from the lengthening of the adult life of the parent insect and the development of the family, for the relations between parents and offspring tend to become so increasingly intimate and interdependent that we are confronted with a new organic unit, or biological entity—a super-organism, in fact, in which through physiological division of labor the component individuals specialize in diverse ways and become necessary to one another's welfare or very existence. Since this integration necessarily leads to an important modification of the activities of the originally solitary insects composing the society it will be advisable to dwell for a few moments on the basic behavior of insects.

The activities of insects, like those of other animals, are an expression of three fundamental appetites or appetencies. Two of these—hunger and sex—are positive and possessive, the other—fear or avoidance—is negative and avertive. These appetites appear as the needs for food, progeny and protection. So far as I am able to see, they manifest themselves in insects in essentially the same manner as in the higher animals, such as birds, mammals and man. The appetites of hunger and sex arise from internal stimuli which compel the organism to make random or trial and error movements till appropriate, specific external stimuli are encountered. Then a sudden, consummatory reaction occurs and the relieved organism lapses into quiescence till the internal stimuli again make themselves felt. In the case of fear or aversion, harmful or disagreeable stimuli, usually of external origin, cause random movements till the organism escapes or succeeds in ridding itself of the noxious or discomfort-producing situation, when it becomes quiescent. And the behavior of insects, like that of other animals, seems to be made up of successions of such appetitive or avertive cycles, which may be repeated during the life-cycle, or—and this is particularly true of insects—the whole life-cycle may consist of a few appetitive cycles of very elaborate patterns—the so-called "instincts."

Now when insects or other animals, for that matter, take to living in societies these fundamental appetites, which as solitary individuals they have been exercising for millions of years, are

by no means lost or suppressed but become peculiarly modified. Since the environment of the social is from the outset much more complex than that of the solitary insect, it must respond not only to all the stimuli to which it reacted in its presocial stage but also to a great number of additional stimuli emanating from the other members of the society in which it is living. Even man, as Berman says, "with the growth of his imagination and the increase in number and density of his surrounding herd, has become the subject of continuous stimulation." The result seems to be a greatly increased responsiveness of the organism. It becomes, so to speak, socially sensitized, and all its appetites and emotions become hypertrophied or even perverted. This will be clear for the insects from the following very summary considerations:

(1.) Social life encounters serious and urgent difficulties in the matter of food, for the colony must have access to a supply which is abundant, nutritious and easily and continuously available in order that all the adult members as well as the young may be adequately nourished. Such an ideal food-supply is rare so that social insects are, as a rule, chronically hungry and in the presence of food positively greedy. Whenever possible both bees and ants gorge themselves to the utmost. While an ant is feeding on nectar or syrup her abdomen may be snipped off with a pair of scissors, without interrupting her repast. We shall see, however, that she appropriates only a very small portion of the swallowed food and that she distributes most of it among her nestmates. Hence, though she behaves like a glutton, we must refrain from regarding her as such. When we see a man importuning everybody for food or money we naturally regard him as avaricious or greedy, but when we learn that he is turning in all his collections to the Red Cross, he is transformed in our estimation. Not only does the social insect thus develop an unusual appetite for food but it also develops elaborate methods of apportioning the food among the adults and brood of the colony according to their various needs. Furthermore, the greatest economy in the use of food, which is of course energy, must be practiced and various methods of preserving and storing it for consumption during seasons of scarcity must be devised. And since insect societies must compete with many other hungry animals they tend to specialize in their diet and to take to foods that can not be readily utilized by other organisms. All this specialization leads eventually to the development of a caste peculiarly adapted to provisioning the colony. As we shall see, this caste comprises the so-called "workers."

(2.) The reproductive gives rise to even more serious difficulties than the nutritive appetite. If all the individuals in the colony are permitted to reproduce without restraint, the popula-

tion will very soon outrun the food-supply and all its members will suffer from malnutrition or starvation, or it will have to resolve itself into smaller and feebler communities, and spread over a larger territory. The higher social insects have overcome this difficulty by rigidly restricting reproduction, except when food happens to be unusually abundant, to a few individuals and suppressing it in all the others. Hence the fecundity of certain females, the queens, and of the males, or drones, becomes greatly enhanced or hypertrophied, while the remaining females, the workers, are reduced to physiological sterility. But it was found most convenient, while thus developing the queens and males as a reproductive and the workers as a nutritive caste, and depriving the latter under normal conditions of the capacity for reproduction, to leave them in possession of their primitive parental instincts, that is, an ardent propensity for nursing the brood.

(3.) In the higher social insects fear is very readily aroused and can be easily studied in all its manifestations from abject cowardice and "death-feigning" in small and feeble species to panic rage in very populous communities. It is certainly of great biological significance, because these insects and their helpless brood are sedentary, or fixed to a particular environment and are therefore exposed to the unforeseen attacks of enemies, inundations of great changes of temperature. Hence, we find that they not only make elaborate nests and fortifications but have developed powerful jaws, hard skulls, pungent or nauseating secretions and deadly stings. The workers originally assumed the protective rôle in addition to their other functions, but in many ants and most termites a special warrior or soldier caste has been evolved. Then, precisely as in man, many wasps, bees and ants found that the best method of defence is offence and their enemies were attacked before they could reach the nest. From this it was, of course, only a step to the organization of marauding and plundering expeditions and the development of aggressive warfare.

All the very complicated manifestations of the hunger, sex and fear appetites are so inextricably interwoven and interdependent that it is impossible adequately to study any one of them in isolation. I shall therefore have to refer to all of them again and again, but I wish to put the main emphasis in these lectures on the hunger appetite, because it is the most fundamental, exhibits the most astonishing developments and is found to have an even greater influence on the reproductive and protective appetites than we had supposed. The recent work of the biochemists and physiologists on the vitamines and internal or endocrine secretions, or "encretions" as some German investigators call them, has shown that extremely minute quantities of certain substances may have very

profound and far-reaching effects on the metabolism, structure and functioning of living animals, and there has long been a suspicion that the differentiation of the fertile and sterile castes among social insects may be due to very delicate chemical stimuli. I shall endeavor to show that such stimuli may also play a determining rôle in maintaining the integrity or solidarity of many insect societies.

Before describing the various societies in greater detail I wish briefly to compare them with human society. I use this word in the singular, because at the present time, owing to the greatly increased facilities of transportation and intercommunication, what were once numerous independent human societies have practically fused or are about to fuse to form one immense, world-wide society. Human and insect societies are so similar that it is difficult to detect really fundamental biological differences between them. This assertion may be supported by the following considerations:

(1.) It is sometimes said or implied that human society is a rational association, due to intelligent cooperation, or contract among its members, whereas insect societies are merely physiological or instinctive associations. The second part of this statement is correct, but he who would seek support for the first part in the works of present day sociologists, psychologists and philosophers will be disappointed. The whole trend of modern thought is towards a greater recognition of the very important and determining rôle of the irrational and the instinctive, not only in our social but also in our individual lives. The best proof of this statement is to be found in the family which by common consent constitutes the primitive basis of our society, just as it does among the insects, and the bonds which unite the human family are and will always be physiological and instinctive.

(2.) It may be said that insect societies are discrete entities, each of which arises as a single family, increases in population for some time and then dies away, whereas human society—the Great Society of Graham Wallas—is a mixtures of families and groups which grow and continue indefinitely. This is an important distinction but not absolute, since human society must have arisen from a single family or a few families, such as we find among the anthropoids. The difference would therefore seem to lie in the fact that our society no longer repeats its earliest phylogenetic stage as does that of the social insects. But there are some insects, such as the honey-bee and some South American bees and wasps, that no longer repeat this incipient stage but from time to time send off new colonies, or societies by swarming, much as did the

Phoenicians and early Greeks and the nations of western Europe in more recent times.

(3.) Korzybski, in an interesting book entitled "The Manhood of Humanity," has recently endeavored to emphasize another difference, the existence of social heredity, or what he calls "time-binding," in human society and its absence among animals. Certainly no one can overestimate the importance of tradition and social heredity. We should still be in the anthropoid stage if we had failed to preserve and add to the capital of culture and mores transmitted to us by former generations or ceased to transmit them and the fruits of our own activities to our descendants. It is clear also that the social insects do not bequeath libraries, institutions and bank accounts to their posterity, and that each colony or society begins anew with the structural and instinctive equipment acquired by true, or organic heredity. This explains why we see so little change in these insects during the past 50 million years. Nevertheless, the distinction is not absolute. There are, as I shall show, ants, termites and beetles that cultivate fungi and bequeath them to succeeding generations. Social insects may also be said to bequeath real estate, that is, their nests, pastures and hunting grounds; and since the young queens of ants and termites often live for some time in the parental nests before they establish colonies of their own, there is reason to believe that they may acquire a very slight amount of experience by consorting with their sisters and parent queen.

(4.) It may be said that the social insects differ from man in not having learned the use of tools, but there are species of ants that use their larvæ as shuttles in weaving the silken walls of their nests, and the marvelous engineering feats of many social insects show that they are our close rivals in controlling the inorganic environment.

(5.) That they have acquired an equally astonishing control of their organic environment is shown by the fact that they are the only animals besides ourselves that have succeeded in domesticating other animals and enslaving their kind. In fact, the ants and termites may be said to have domesticated a greater number of animals than we have, and the same statement may prove to be true of their food-plants, when they have been more carefully studied.

(6.) It may be maintained that we have developed language and this, of course, is a true distinction, if we mean by language articulate speech, but the members of an insect society undoubtedly communicate with one another by means of peculiar movements of the body and antennæ, by shrill sounds (stridulation) and by odors.

The wonder has always been, not that there are so many differences in structure between such disparate organisms as insects and man, but that there are so many striking similarities in behavior. And the wonder grows when we find that social organization at least incipiently analogous to our own has arisen *de novo* on at least 24 different occasions in nearly as many natural families or subfamilies belonging to five very different orders of insects. A list of the groups that form these various societies is given in the accompanying table.

Coleoptera (Gynandrarchic)	1. Scarabæidæ (Copris, Minotaurus)
	2. Passalidæ (Passalus)
	3. Tenebrionidæ (Phrenapates)
	4. Silvanidæ (Tachigalia Beetles)
	5. Ipidæ (Ambrosia Beetles)
	6. Platypodidæ (Ambrosia Beetles)
Hymenoptera (Gynarchic)	*Sphecoidea*
	7. Sphecidæ (Sphex)
	8. Bembicidæ (Digger Wasps)
	Vespoidea
	9. Eumeninæ (Synagris)
	10. Zethinæ (Zethus)
	*11. Stenogastrinæ (Stenogaster)
	*12. Epiponinæ (Chartergus, Belonogaster, etc.)
	*13. Rhopalidiinæ (Rhopalidia, etc.)
	*14. Polistinæ (Polistes)
	*15. Vespinæ (Vespa)
	Apidæ
	16. Halictinæ (Halictus)
	17. Ceratininæ (Allodape)
	*18. Bombinæ (Bumble-bees)
	*19. Meliponinæ (Stingless Bees)
	*20. Apinæ (Honeybees)
	*21. Formicidæ (Ants)
Dermaptera (Gynarchic)	22. Forficulidæ (Earwigs)
Embidaria (Gynarchic)	23. Embiidæ (Embia)
Isoptera (Gynandrarchic)	*24. Termitidæ (Termites, or "White Ants")

In this list the first to tenth, the sixteenth and seventeenth, and the twenty-second and twenty-third are incipiently social or subsocial; the remaining ten, marked with asterisks, are definitely social. In the termites and all the beetle groups the colony consists of a male and female parent and their offspring of both sexes; in all the Hymenoptera, Dermaptera and Embidaria the female alone founds the colony, which is developed by her daughters. The former groups are therefore gynandrarchic, the latter gynarchic. These differences will become clearer as we proceed.

Let us examine first the six beetle societies which have been developed by species belonging to as many different natural families.

(1.) *Scarabæidæ*—For our knowledge of the habits of the dung-beetles we are indebted to one of the greatest entomologists, J. H. Fabre. His observations are recorded in parts of four of the ten volumes of his "Souvenirs Entomologiques," and comprise some of their most remarkable chapters. Some notion of the difficulties which he encountered while working out the life-histories of these insects may be gleaned from his statement that he did not succeed in completely elucidating the habits of one of them, the sacred Scarabæus, till he had had it under observation for nearly forty years. He studied quite a number of species and found startling diversity in their behavior. Some of them, the Aphodii, e. g., merely lay their eggs in fresh dung and the hatching larvæ feed on the substance. Among the others, which resort to much more elaborate methods of caring for their progeny, three different types of behavior may be distinguished:

(A.) The Sacred Scarabæus (Fig. 1) above mentioned and many allied forms are fond of the open sunlight and are often seen making perfect spheres of fresh cattle manure and trundling them away to cavities in the soil or under stones. These pellets are devoured by the beetles. Fabre found that a single beetle will not only eat but digest a mass of dung equal to its own body-weight in 12 hours. When the female beetle is ready to lay she makes a very similar pellet, but this time of sheep's dung and rolls it into an elliptical chamber which she has previously excavated in the

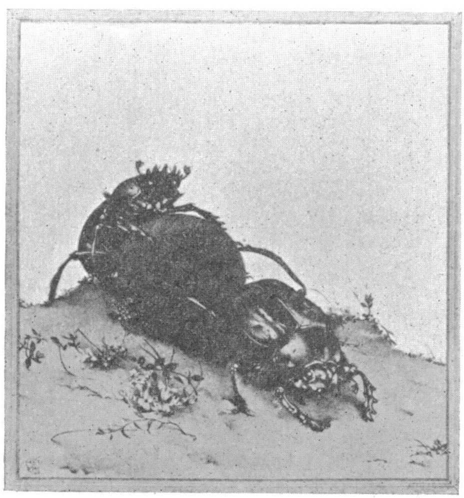

FIG. 1
Sacred scarabæi (Scarabæus sacer) trundling their pellet of dung. After E. J. Detmold.

soil. This chamber is about as large as one's fist. She then makes a crater-shaped depression surrounded by a circular flange at one pole of the pellet, lays a large egg in it and draws the material of the flange over it till it is completely enclosed. The pellet is now pear-shaped. Thereupon the mother beetle leaves the chamber and proceeds to dig another and provision it in the same manner. The hatching larva consumes the inside of the pellet, pupates

FIG. 2
Male Sisyphus beetle (*Sisyphus schæfferi*) holding the dung pellet while the female digs the burrow to receive it. After E. J. Detmold.

within it and emerges as a beetle in due season. There is, of course, nothing social about this insect. But in a smaller, allied form, *Sisyphus schæfferi* (Fig. 2), Fabre found that the male helps the female trundle her pellet to a convenient spot, guards it while she excavates a cavity, assists her in lowering the pellet, waits for her till she has oviposited in it in the same manner as the Scarabæus, and then departs with her to repeat the performance.

(B.) In Copris, of which Fabre studied two species, *C. hispanus* and *C. lunaris,* we have a closer approach to a social condition. These insects are crepuscular and dig a chamber as large as a large apple immediately under the pile of dung. This is then carried down in masses and leisurely devoured. During the breeding season, however, the beetles associate in pairs and the male and female not only cooperate in excavating a chamber but also in nearly filling it with dung, which they then proceed to knead into the form of a smooth ellipsoid as large as a turkey's egg (Fig. 3). In the case of *C. hispanus* the male then deserts the female and the latter proceeds to cut the ellipsoid up into four spherical pellets, each of which is treated like the pellet of the

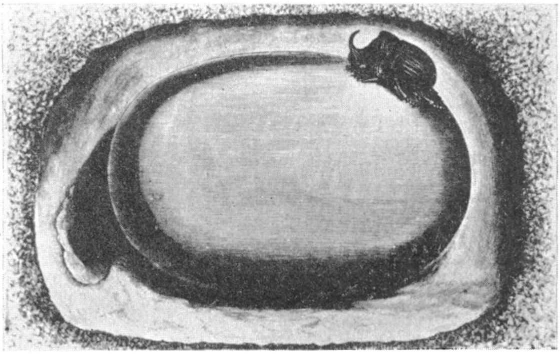

FIG. 3
Spanish Copris (*Copris hispanus*) fashioning her large ellipsoid of dung in her subterranean chamber. After J. H. Fabre.

sacred Scarabæus, provided with an egg and converted into a regular ovoid (Fig. 4). The mother remains in the chamber, guarding the pellets and keeping them free from fungus growth for four months, while the larvæ are developing within them. After the young beetles hatch the mother accompanies them to the surface of the soil and the family disperses. In the case of *C. lunaris* the male remains in the chamber with the female and helps her manufacture the ovoids, which owing to his assistance are twice as numerous as they are in *hispanus*. When the young beetles emerge they are escorted to the surface by both parents.

(C.) Other beetles, like Geotrypes, Onthophagus and Minotaurus, dig long tubular tunnels into the soil immediately under the dung. As a rule, they do not make spherical pellets but pack the deeper, blind end of the burrow with layers of dung till it forms

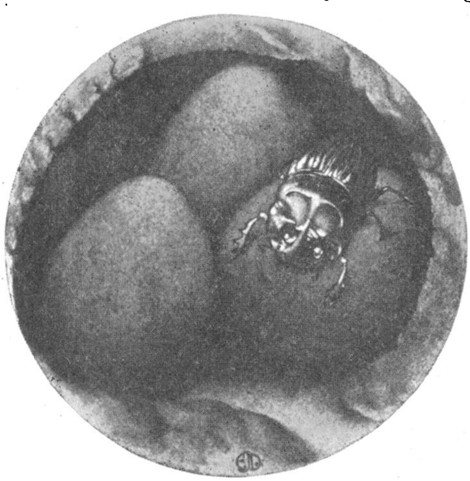

FIG. 4
Spanish Copris (*Copris hispanus*) guarding her ovoids of dung in the subterranean chamber. After E. J. Detmold.

a sausage shaped mass above the egg or enclosing it at one end. The behavior of *Minotaurus typhœus* (Fig. 5) is even more astonishing than that of Copris. The male and female beetles mate in March and together dig a tubular gallery straight down into the soil to the remarkable depth of five feet. The male remains above, works the dung up into elliptical pellets and lowers them down the shaft, while the female, after laying an egg in the sand at the bottom of the burrow, receives the pellets, tears them apart and packs the fragments down, as if she were working in a silo, till they form a mass as big as one's finger. Then she digs in succession a few branch galleries off from the main shaft, furnishes each of them with an egg and provisions it in the same manner. By constructing an ingenious apparatus and providing the beetles with an unlimited supply of manure, Fabre induced one male to make

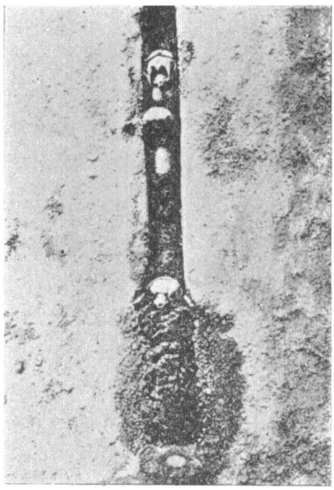

FIG. 5
Lowermost portion of burrow of the Minotaur (*Minotaurus typhœus*) showing the male bettle lowering the dung in pellets and the female storing it in layers above her egg. After J. H. Fabre.

239 pellets and hand them down to the female, but unfortunately the latter had died at the bottom of the gallery, so that there were no eggs and the pellets had not been torn apart and stored. The development of the young requires five months and the female very probably remains in the burrow till the brood hatches and crawls up to the surface.

(2.) *Passalidæ*—These large, active, jet-black, flattened and parallel-sided beetles (Fig. 6) are common throughout the tropics of both hemispheres. A single species, *Passalus cornutus,* occurs in the United States as far north as Michigan and Massachusetts. Ohaus, who first studied the habits of several species in the forests

of Brazil, has shown that they form colonies consisting of a male and female and their progeny and make large, rough galleries in rather damp, rotten logs. The broadly elliptical yellowish green or greenish black eggs, to the number of a dozen or more, are laid in a loose cluster and guarded by the parents. The larvæ are drab-colored and cylindrical, with the hind pair of legs reduced to peculiar short paw-like appendages which can be rubbed back and forth on striated plates at the bases of the middle legs (Fig. 7), thus producing a shrill note. On the dorsal surface of the abdomen of the adult beetle there is also a stridulatory organ in the form of patches of minute denticles which may be rubbed against similar structures on the lower surfaces of the wings. Ohaus found that the parent beetles triturate the rotten wood and apparently

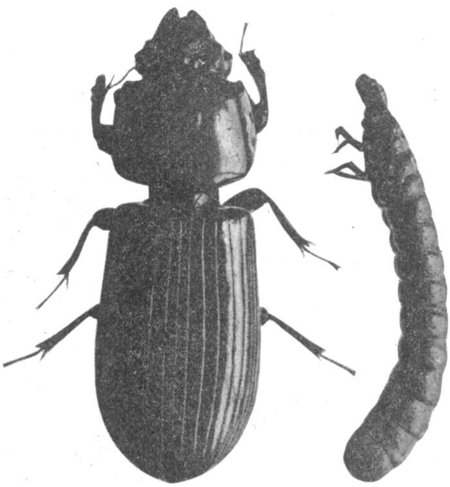

FIG. 6
Passalus sp. Adult beetle and rather young larva, about twice natural size.

treat it with some digestive secretion which makes it a proper food for the larvæ, since their mouth-parts are too feebly developed to enable them to attack the wood directly. They are therefore compelled to follow along after their tunnelling parents and pick up the prepared food. All the members of the colony are kept together by stridulatory signals. The noise made by the beetles is so loud that it is possible to detect the presence of a Passalus colony in a log by merely giving it a few sharp raps. I have been startled on more than one occasion in Central America by the shrill response thus elicited from large Passali that were burrowing deep in the wood. When the larvæ are mature they pupate in the burrows and the emerging beetles are guarded and fed by the parents till they are fully mature. Observations that I have made in Australia,

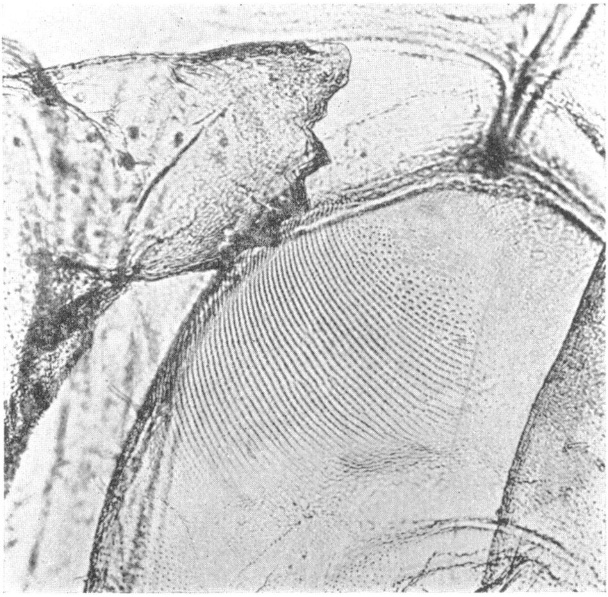

FIG. 7
Microphotograph showing abbreviated, paw-like hind leg of Passalus larva and the striated surface over which its toothed edge is rubbed during stridulation.

Central America, Trinidad and British Guiana confirm Ohaus's statements.

(3.) *Phrenapates*—Nearly a century ago Kirby described a

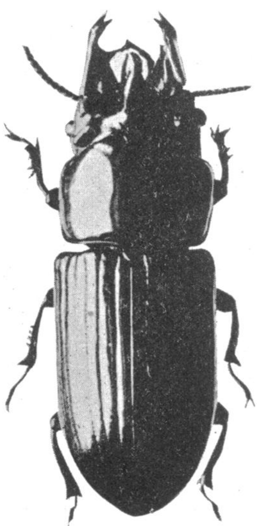

FIG. 8
Phrenapates Bennetti, a social Tenebrionid beetle, from a specimen in the Museum of Comparative Zoology. Photograph by Mr. Leland H. Taylor.

peculiar beetle from Colombia as *Phrenapates bennetti* (Fig. 8). It is about an inch long, jet-black and shining and superficially resembles Passalus, but belongs to a very different family, the Tenebrionidæ. G. C. Champion records it from Central America (Panama to Guatemala), and states that he "met it in plenty in decaying timber in the humid forest region of Chiriqui and frequently dug it out of cylindrical burrows, probably made by the larvæ, in the solid wood." Some years later Ohaus encountered the insect in Ecuador and gave a more detailed account of its habits. The male and female gnaw in the wood of the silk-cotton tree (Bombax) a narrow, cylindrical gallery about a foot and a half long and make roomy niches on each side of it at definite intervals. All the work is neat and smooth, unlike the burrow of Passalus. In each of the niches Ohaus found an egg or one or two larvæ, the latter feeding on fine, elongate shaving which filled the niches and had evidently been provided by the parent beetles. The eggs are laid at rather long intervals so that the larvæ, unlike those of Passalus, vary considerably in size. They resemble our common meal-worms (*Tenebrio molitor*), but are milk-white. No stridulatory organs could be detected in the beetles, but like some other Tenebrionids (Blaps) they emit a penetrating odor.

(4.) *Tachigalia Beetles*—During the summer of 1920 I discovered in the jungles of British Guiana a couple of Silvanid beetles which lead a more spectacular existence than some of the preceding. These beetles, which Messrs. Schwarz and Barber have named *Coccidotrophus socialis* and *Eunausibius wheeleri* (Fig. 9) are less than a quarter of an inch in length and have long, slender, subcylindrical, red or chestnut brown bodies, with short legs and club-shaped antennæ. They occur only in the hollow leaf-petioles (Fig. 10) of a very interesting tree, *Tachigalia paniculata*, and only in young specimens $1\frac{1}{2}$ to 7 ft. high while they are growing in the shade under the higher trees of the jungle. The older trees, which

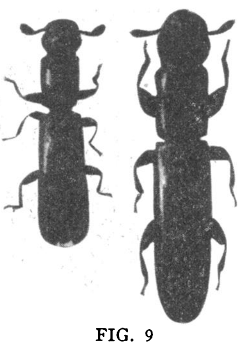

FIG. 9
Tachigalia beetles, the larger *Coccidotrophus socialis*, the smaller *Eunausibius wheeleri*.

may attain a height of 40 feet or more, have all their petioles inhabited by viciously stinging or biting ants. Each beetle colony is started by a male and female which bore through the wall of the petiole, clean out any pith or remains of previous occupants it may contain and commence feeding on a peculiar tissue rich in proteins, which is developed in parallel, longitudinal strands in the wall of the petiole (Figs. 11 and 12). As they keep gnawing out this tissue they gradually make grooves and pile their feces on the ungnawed intervening areas, so that the interior of the petiole assumes a peculiar appearance (Figs. 13 and 14). While the beetles are thus engaged numbers of small mealy-bugs of the genus

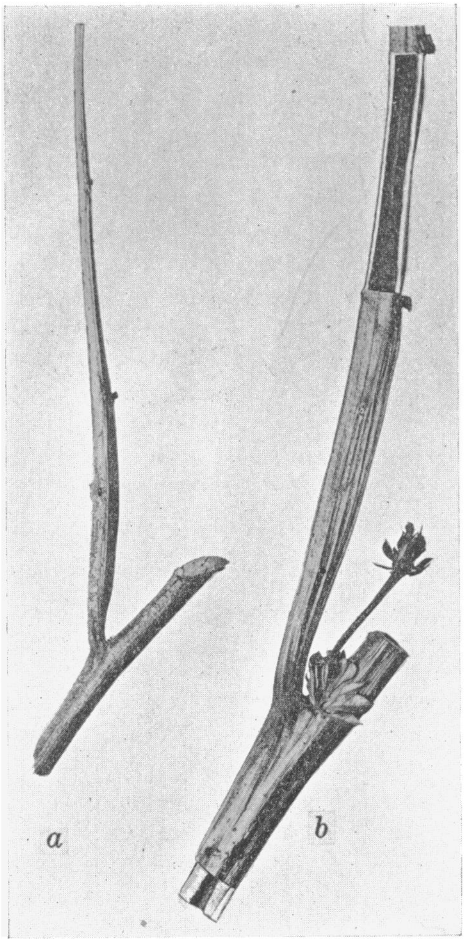

FIG. 10
Bases of leaf-petiole of *Tachigalia paniculata* (*a*) of young, shade tree; (*b*) of large, sun tree, both nearly one-half natural size. Pieces of the older petiole and adjacent trunk have been cut out to show the cavity.

Pseudococcus (*Ps. bromeliæ*) (Fig. 15), covered with snow-white wax, wander into the petiole through the opening made by the beetles, settle in the grooves, sink their delicate sucking mouth-parts into the nutritive tissue and imbibe its juices. The beetles soon begin to lay their small, elliptical, white eggs along the edges of the grooves (Fig. 14) and the hatching larvæ, which are beautifully translucent, run about in the cavity and feed on the same tissue as the parents. But incredible as it may seem both the adult beetles and the larvæ in all stages have learned to stroke the mealy-bugs with their antennæ, just as our common ants stroke similar mealy-bugs and plant-lice, and feed on the droplets of honey dew,

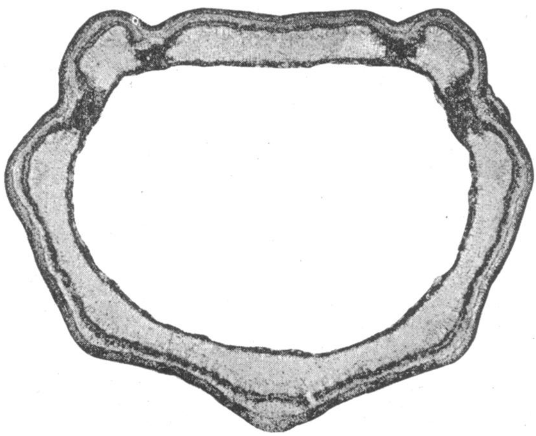

FIG. 11

Cross-section of base of a young, uninhabited petiole of *Tachigalia paniculata* showing the bands of protein-containing nutritive tissue (dark). Photograph by Professor I. W. Bailey.

or saccharine excrement which they give off when their backs are properly titillated. So greedy are the Silvanids for this nectar that I have seen a beetle or a larva stroke a mealy-bug for an hour or longer and receive and swallow a drink every few minutes. When two or more beetles or two or more larvæ or a group of beetles and larvæ happen to be engaged in stroking the same mealy-bug, they stand around it, like so many pigs around a trough, and the larger or stronger individual keeps butting the others away with its head. The butted individuals, however, keep returning and resuming their stroking till the knocks become too severe or the stronger individual leaves and begins to stroke another mealy-bug. Thus the beetles and their progeny have discovered a rich food supply, consisting in part of the proteid-containing tissues of the Tachigalia and in part of the sugar and water discharged by the mealy-bugs, which in turn imbibe the sap of the tree. The beetles lay their eggs at intervals so that larvæ in all stages are

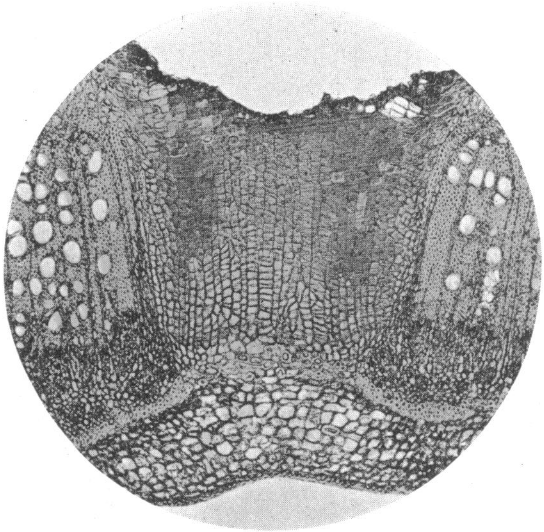

FIG. 12
Enlargement of one of the bands of nutritive tissue of the preceding figure, showing the rather homogeneous protein-containing cells. Microphotograph by Professor I. W. Bailey.

found in the same colony. When mature each larva constructs a cocoon of minute particles bitten out of the plant tissues (Fig. 16), creeps into it, closes the opening from the inside and pupates. When the young beetles hatch they remain with their parents and

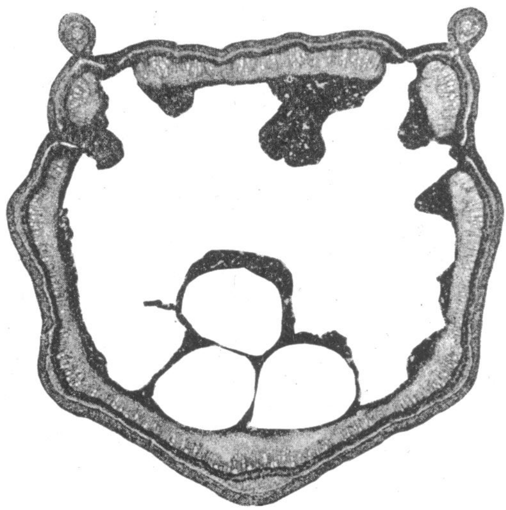

FIG. 13
Cross-section of Tachigalia petiole inhabited by a flourishing colony of *Coccidotrophus socialis.* The gnawed out areas of nutritive tissue are seen above, with the frass piled on the intermediate areas; below three cocoons have been sectioned. Photograph by Professor I. W. Bailey.

soon begin to lay eggs, so that eventually the colony consists of several dozen beetles, larvæ, pupæ and mealy-bugs in all stages and all living peacefully together, except for the little family bickerings of the beetles and larvæ over the milking of their patient, snow-white cattle. When the petiole becomes too crowded, pairs of young beetles leave it, enter other petioles of the same

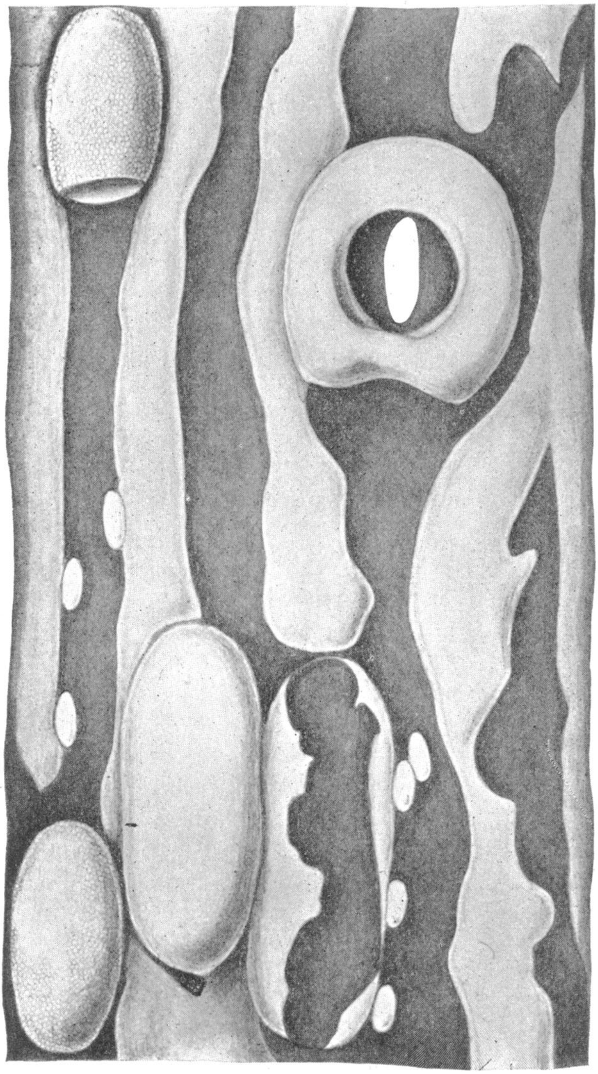

FIG. 14
Enlarged drawing of a part of the wall of a *Tachigalia* petiole inhabited by *Coccidotrophus socialis;* showing the food grooves and frass ridges, the entrance with its wall, the eggs, an intact and broken cocoon of the *Coccidotrophus* and two cocoons of the Coccid parasite, *Blepyrus tachigaliæ,* one of them after the eclosion of the parasite.

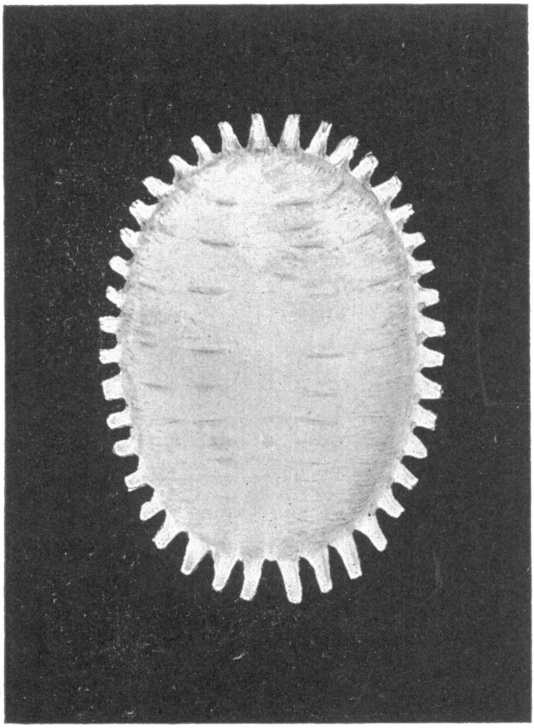

FIG. 15
Pseudococcus bromeliæ Bouché. Sketch of an adult living female with intact covering and peripheral pencils of wax.

or other Tachigalia trees and start new colonies. As the tree grows and emerges from the undergrowth into the sunlight, the ants which then take complete possession of it oust the beetles from the petiolar cavities but adopt their mealy-bugs, just as the invading German army appropriated the French cattle. There are many other extraordinary insects associated with the Tachigalia, its beetles and mealy-bugs, but I must omit an account of them because they are irrelevant to the present discussion.

(5.) *Ipid Ambrosia Beetles*—The family Ipidæ comprise small, cylindrical, red-brown or black beetles which live in the trunks and branches of trees. The group is now divided into two sections, one of which includes the bark-beetles, which are nonsocial and make the beautiful, radiating burrows so commonly seen on the inner surface of the bark of sickly trees, the other includes the ambrosia beetles (Fig. 17), which are social and run their burrows right into the wood of healthy or recently felled trees. The name "ambrosia beetles" is derived from a term applied by Schmidberger to the fungi which the beetles cultivate as food for themselves and their

larvæ. Structurally the two sections of the family Ipidæ can be readily distinguished by the mouthparts, the bark-beetles having their maxillæ armed with a row of 12 to 20 strong tooth-like bristles adapted to gnawing bark, whereas the maxillæ of the ambrosia beetles are fringed with 30 to 40 delicate, curved bristles, evidently suited to cropping the soft hyphæ of their food-fungus. Fourteen genera and nearly four hundred species of ambrosia beetles have been described. One genus alone, Xyleborus, which is cosmopolitan, contains 246 species. The fungi that grow in the galleries often

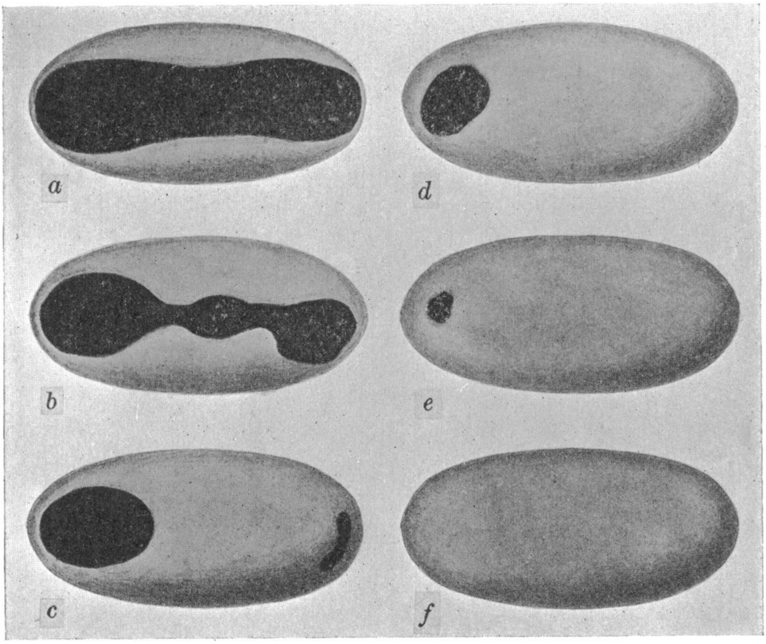

FIG. 16
Six successive stages in the construction of the cocoon by the full-grown larva of *Coccidotrophus socialis.*

give their walls a black stain, so that the value of the wood thus affected is greatly impaired. One species, *Xyleborus perforans,* has a bad reputation in the tropics, where it goes by the name of "tippling Tommy," because it has a strong predilection for boring in the staves of wine, beer and rum casks and thus causing much leakage. It might be adopted by our prohibitionists as their totem-animal.

The ambrosia beetles were first carefully studied in this country by H. G. Hubbard, whose untimely death deprived us of one of our most talented entomologists. I can not do better than quote his concise account of two of our species of Pterocyclon (*mali*

and *fasciatum*): "The sexes are alike, and the males assist the females in forming new colonies. The young are raised in separate pits or cradles which they never leave until they reach the adult stage. The galleries, constructed by the mature female beetles, extend rather deeply into the wood, with their branches mostly in a horizontal plane. The mother beetle deposits her eggs singly in circular pits which she excavates in the gallery in two opposite series, parallel with the grain of the wood. The eggs are loosely packed in the pits with chips and material taken from the fungus bed which she has previously prepared in the vicinity and upon which the ambrosia has begun to grow. The young larvæ, as soon as they hatch out, eat the fungus from these chips and eject the refuse from their cradles. At first they lie curled up in the pit

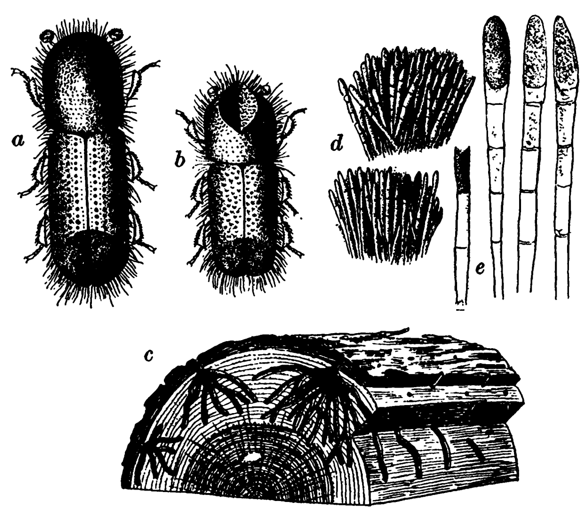

FIG. 17
Ambrosia beetle, *Xyleborus celsus* Eichh., of the hickory (after Hubbard); *a*, female beetle; *b*, male; *c*, piece of hickory, showing burrows of *X. celsus* in the sap-wood; *d*, ambrosia grown by *X. celsus* on the walls of of the burrows; *e*, same more enlarged.

made by the mother, but as they grow larger, with their own jaws they deepen their cradles, until, at full growth, they slightly exceed the length of the larvæ when fully extended. The larvæ swallow the wood which they excavate, but do not digest it. It passes through the intestines unchanged in cellular texture, but cemented by the excrement into pellets and stained a yellowish color. The pellets of excrement are not allowed by the larvæ to accumulate in their cradles, but are frequently ejected by them and are removed and cast out of the mouth of the borings by the mother beetles. A portion of the excrement is evidently utilized to form

the fungus bed. The mother beetle is constantly in attendance upon her young during the period of their development, and guards them with jealous care. The mouth of each cradle is closed with a plug of the food fungus, and as fast as this is consumed it is renewed with fresh material. The larvæ from time to time perforate this plug and clean out their cells, pushing out the pellets of excrement through the opening. This debris is promptly removed by the mother and the opening again sealed with ambrosia. The young transform to perfect beetles before leaving their cradles and emerging into the galleries." The ambrosia of Pterocyclon "is moniliform and resembles a mass of pearly beads. In its incipient stages a formative stem is seen, which has short joints that become globular conidia and break apart. Short chains of cells, sometimes showing branches, may often be separated from the mass. The base of the fungous mass is stained with a tinge of green, but the stain of the wood is almost black.

(6.) *Platypodid Ambrosia Beetles*—These were formerly included among the Ipidæ but are now regarded as an independent family. They can be easily distinguished by their much broader head and longer feet, the first joint of the tarsi being as long as all the remaining joints together. The great majority of the species are tropical, so that their habits have not as yet been very thoroughly studied. So far as known, the Platypodids all bore in the wood of dying or recently felled trees, live in societies and feed on fungi which they grow on the walls of their burrows. Hubbard and Swaine have studied some of our North American and Strohmeyer has published some observations on one of the few European forms. The following description of *Platypus compositus* is quoted from Hubbard: "They are powerful excavators, generally selecting the trunks of large trees and driving their galleries deep into the heart-wood. They do not attack healthy trees but are attracted only by the fermenting of the sap of dying or very badly injured trees. The death rattle is not more ominous of dissolution in animals than the presence of these beetles in standing timber. . . . The female is frequently accompanied by several males and as they are savage fighters, fierce sexual contests take place, as a result of which the galleries are often strewn with fragments of the vanquished. The projecting spines at the ends of the wing-cases are very effective weapons in these fights. With their aid a beetle attacked in the rear can make a good defense and frequently by a lucky strike is able to dislocate the outstretched neck of his enemy. The females produce from 100 to 200 elongate-oval pearl-white eggs, which they deposit, in clusters of 10 or 12, loosely in the galleries. The young require five or six weeks for

their development. They wander about in the passages and feed in company upon the ambrosia which grows here and there upon the walls. . . . The older larvæ assist in excavating the galleries, but they do not eat or swallow the wood. The larvæ of all stages are surprisingly alert, active and intelligent. They exhibit curiosity equally with the adults, and show evident regard for the eggs and very tender young, which are scattered at random about the passages, and might easily be destroyed by them in their movements. If thrown into a panic the young scurry away with an undulatory movement of their bodies, but the older larvæ will frequently stop at the nearest intersecting passage and show fight to cover their retreat.'' The ambrosia of *P. compositus* consists of hemispherical conidia growing in clusters on branching stems. The long continued growth of this fungus blackens the walls of the older galleries.

Each species of ambrosia beetle—and this is true of both the Ipidæ and the Platypodidæ—grows its own peculiar fungus in a pure culture, irrespective of the tree it may select for its burrows. Strohmeyer seems to have shown how in the case of certain Platypodids the mother beetle manages to obtain the spores of the particular fungus which she cultivates. He finds that she carries them from the burrows in which she passed her larval and pupal stages to the new burrows which she makes for her own progeny in a kind of crate or basket consisting of one or several dense tufts of long, curved hairs on the top of her head or on her mouth-parts; and Schneider-Orelli has found that the females of the Ipid ambrosia beetles carry the fungus in the fore part of the stomach and are thus able to infect the walls of the new burrows which they establish. These are only two of the instances among the social insects of the actual transmission of a food-plant from generation to generation.

We may now summarize very briefly the main points of interest in connection with the social beetles:

(1.) The six unrelated families are all very ancient. Species of four of them (Silvanidæ, Tenebrionidæ, Ipidæ and Platypodidæ) are, in fact, known from the Baltic Amber. The absence of the dung-beetles from that formation is easily explained, since these insects are not arboreal, nor are they attracted by liquid resins. Several of the living genera (Scarabæus, Copris, Onthophagus, Sisyphus, and Gymnopleurus), however, are known from the Upper Miocene shales of Oeningen, and Hagedorn mentions several species of ambrosia beetles as occurring in the African and Malagasy copal, a fossil resin of comparatively recent formation. There can be little doubt that all the six families which I have been consider-

ing are much older than these records would seem to indicate. Most of them, in fact, are cited by Handlirsch as probably having arisen at the beginning of the Cretaceous or even earlier.

(2.) The substances on which the six groups of social beetles feed are remarkably diverse, ranging from dung and wood in various stages of decay to the living tissues of plants, the honey-dew of mealy-bugs and delicate fungi. These are all abundant and ubiquitous substances of vegetable origin, and all the social beetles manage to store or find their food in such peculiar places that they can avoid intense competition with most other organisms.

(3.) This abundant but in many cases not very nutritious food-supply which the adult beetles seek and exploit primarily for their own consumption enables them to acquire a considerable longevity, and this in turn, of course, enables them to survive the hatching and development of their young.

(4.) In all the groups the parent beetles show a very pronounced interest in their offspring, and feed them directly or, at any rate, place them in close contact with the food and guard them.

(5.) The father beetle cooperates to a greater or less extent with the mother beetle in providing for the young, although his cooperation may be slight. Probably it is really *nil* in most of the Ipid ambrosia beetles, the males of which are in many species wingless and very rare, so that mating must take place in the maternal colony.

(6.) There are neither structural nor physiological differences between the fully developed young and the adult parents of the social beetles. In other words, nothing like a development of castes has made its appearance among them.